

EMBRYOLOGY OF *JUBAEOPSIS CAFFRA* BECC.: 3. ENDOSPERM AND EMBRYOGENY

B. L. ROBERTSON

(Department of Botany, University of Port Elizabeth)

ABSTRACT

Initially the endosperm is free nuclear, but in the mature seed it is cellular. Wall formation, which results from cell plate formation, is initiated when the embryo is between 32 and 64 cells large.

The zygote of *J. caffra* undergoes a post-fertilization rest period of between 30 and 70 days prior to division. Embryogeny, which is of the Asterad Type (*Muscari* Variation) is discussed in terms of the systems of Johansen and Souèges. A recapitulatory table for the first four cell generations is presented.

UITTREKSEL

EMBRIOLOGIE VAN *JUBAEOPSIS CAFFRA* BECC.: 3. ENDOSPERM EN EMBRIO-GENIE

Aanvanklik is die endosperm vry-nukleêr maar in die volwasse saad is dit sellulêr. Wandvorming, wat as gevolg van selplaat ontwikkeling geskied, is geïnisieer wanneer die embrio uit tussen 32 en 64 selle bestaan.

Na bevrugting ondergaan die sigoot van *J. caffra* 'n rusperiode van tussen 30 en 70 dae voordat dit verder deel. Embriogenie, wat van die Asterad Tipe (*Muscari* Variasie) is, word in terme van die sisteme van beide Johansen en Souèges bespreek. 'n Rekapitulasietafel vir die eerste vier selgenerasies word voorgestel.

INTRODUCTION

Currently available literature pertaining to *Jubaeopsis caffra* deals almost exclusively with the distribution and general morphology of this species (Beccari, 1913; Marloth, 1915; Long, 1950; Barry, 1957; Story, 1959; Wager, 1968; Wicht, 1969; Palmer & Pitman, 1972; Robertson & Visagie, 1975). The only available data concerning embryological aspects of *J. caffra* are in respect of sporogenesis and gametogenesis (Robertson, a, b, 1976), and to date, nothing on its embryogeny has been published.

In all the reported cases concerning the endosperm of palms generally, it is initially nuclear (Davis, 1966) but subsequently becomes cellular. Some variations do exist in respect of the extent to which the endosperm becomes cellular and the transition from nuclear to cellular endosperm is not complete in all species. In *Cocos nucifera* for example, a large percentage of the endosperm remains in a liquid state, i.e. free nuclear (Cutter, Wilson & Freeman, 1955). In *Areca catechu* on the other hand, the entire mass of nuclear endosperm develops into a very hard cellular tissue (Datta, 1955).

Accepted for publication 24th October, 1975.

Two conflicting reports concerning the endosperm found in *J. caffra* have been published. Marloth (1915) states that the mature seed is without milk, i.e. without nuclear endosperm. Story (1959) disagrees and claims that, just like the coconut, nuclear endosperm is found in the mature *J. caffra* seed.

When discussing the endosperm of palms, the question of ruminations or of ruminant endosperm naturally arises. Again, certain species exhibit this characteristic, e.g. *Areca catechu* (Venkato Rao, 1955) while many others do not.

The development of the palm embryo is still a virtually uninvestigated field of study. By 1950 (Johansen, 1950) the Palmae were embryogenically totally unknown. Subsequent to Johansen's classic publication, a small number of descriptions concerning the embryogeny of the Palmae have become available.

According to Venkato Rao (1958) the embryo development of both *Actinophloeus macarthii* and *Areca catechu* is of the *Trifolium* variation of the Onagrad Type (Johansen, 1950). In this type the basal cell, cb, of the two celled pro-embryo forms the suspensor only and does not contribute to the components of the embryo proper.

Guignard (1961) on the other hand, studied the embryogeny of *Chamaerops humilis* L. and describes the embryo development as belonging to the First Period Megarchtype IV with a Series A1 tetrad in the second cell generation (Souéges 1939, 1948, & 1951, cited by Crété, 1963). This is in fact the first description of an embryo in which the basal cell of the 2-celled proembryo divides by means of a longitudinal wall during the formation of the cells of the second generation. Davis (1966) describes the embryogeny of *Chamaerops* as being of the Asterad Type (Johansen, 1950). Strictly speaking this is incorrect as the proembryo tetrad (second cell generation) of the Asterad Type comprises three tiers: two juxtaposed cells which originate from ca in the 2-celled proembryo; and two superposed cells (m and ci) which originate from cb of the 2-celled proembryo. Johansen's (1950) system for classifying embryonomic types does in fact not provide for a case where the basal cell of the first cell generation divides by means of a vertical or longitudinal wall.

The question concerning embryonomic types in general and the classification thereof is still very much an open question and is dealt with further in the discussion.

In this study three aspects of the embryogeny of *J. caffra* were investigated, viz. embryogenesis, embryotectonics and embryogeneity. For the classification of the embryonomic type both Johansen's and Souéges' systems were used. Furthermore, a comparative study of the size and rate of growth of the fruit and the development of the embryo was made.

MATERIAL AND METHODS

Female flowers and fruits were collected at various developmental stages from a cultivated tree in St. George's Park, Port Elizabeth. This material was fixed and

stored in Craf II (Sass, 1958) prior to dehydration in an ethyl alcohol/tertiary butyl alcohol (TBA) series. Thereafter it was infiltrated with and embedded in paraffin wax (55°C).

Lignification of the endocarp made it impossible to study embryogeny without prior removal of the embryo from the seed. This was achieved by firstly removing the fibrous exo – and mesocarp and then excising the embryo through the single functional germination pore. (Only one ovule remains functional and thus only one germination pore penetrates through the stony endocarp).

The embedded material was sectioned at 10 μ m on a rotary microtome as prescribed by Brooks, Bradley and Anderson (1950) and stained in safranin/fast green (Holtzhausen, 1972).

RESULTS AND DISCUSSION

Endosperm

The fertilization of the secondary nucleus by one of the male gametes results in the formation of the primary endosperm nucleus. (Fusion of the two polar nuclei occurs prior to fertilization.) This nucleus divides without the formation of a cell wall and consequently the endosperm of *J. caffra* is of the nuclear type. Development of the endosperm is initiated some considerable time prior to division of the zygote.

The endosperm nuclei become organised in a thin peripheral layer while the central zone of the embryo sac is filled with a mass of colourless cell sap (Fig. 1). In the mature fruit the peripherally placed endosperm is comprised of a cellular tissue while the central liquid mass becomes absorbed and makes way for a large cavity.

Division of the nuclei of the endosperm *Cocos nucifera* has been interpreted in various ways. Dutt (1954) and Datta, née Dutt (1955) report regular mitotic divisions in the endosperm nuclei, while Cutter and Freeman (1955, cited by Maheshwari, 1963) state that division of these nuclei occurs by means of nuclear fragmentation or amitotic division.

In *J. caffra* there is no doubt that division takes place by means of regular mitotic division (Fig. 2). Figure 1 shows that the division of the nuclei in the peripheral layer appears to be more or less synchronous.

Cell-wall formation in the endosperm is not initiated until the embryo has reached the 32 to 64-celled stage. This is in contrast to some of the other palms, e.g. *Actinophloeus* where the endosperm already becomes cellular at about the eight to ten-celled proembryo stage (Venkato Rao, 1958). Also different is the mode of wall formation. In *Actinophloeus*, the endosperm initially becomes cellular by a process of vacuolation and thereafter by cell plate formation (Venkato Rao, 1958) while in *J. caffra* the very first cell walls result from cell plate formation (Fig. 2).

The divisions are mainly periclinal in relation to the embryo sac wall (Fig. 2)

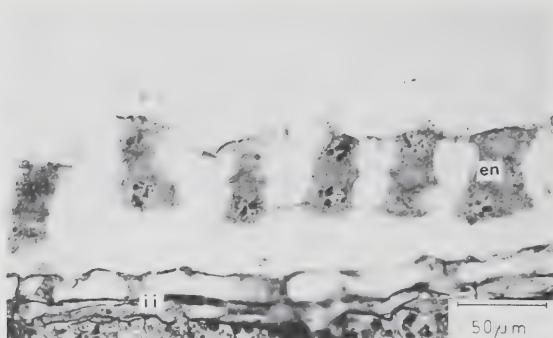


FIG. 1

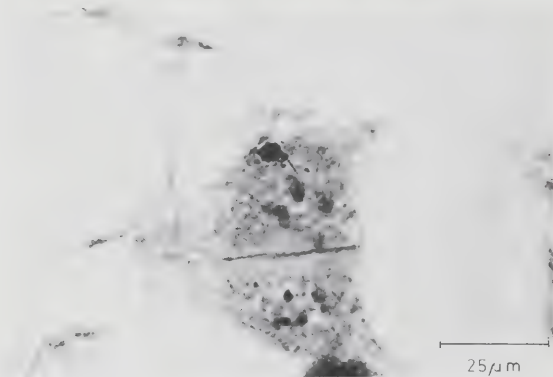


FIG. 2

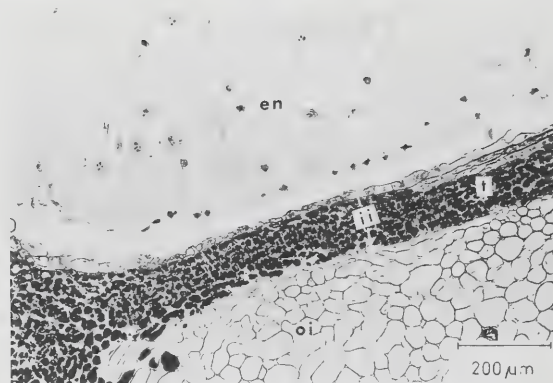


FIG. 3

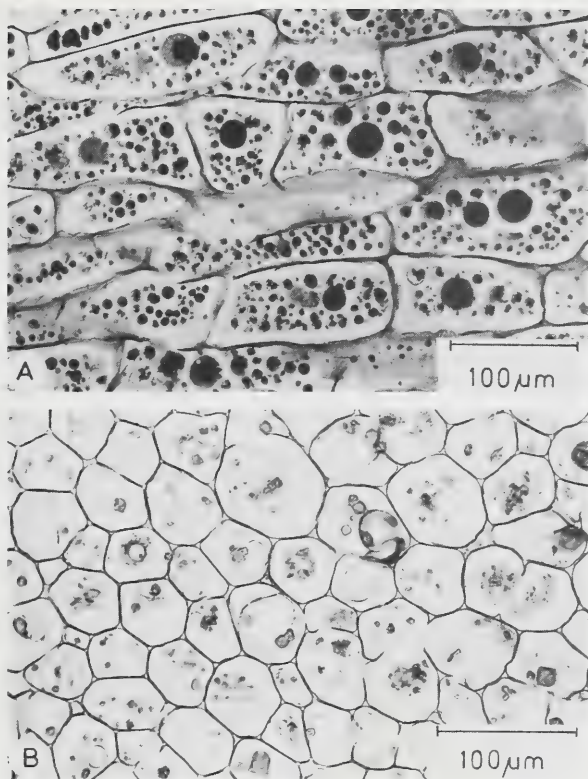


FIG. 4.

Endosperm of a mature *J. caffra* seed. A—Transverse section through the kernel. B—Tangential section through the kernel.

and result in a rather uniform layer of cells being formed. In a young fruit the peripheral endosperm cells are relatively small while the cells towards the middle of the endosperm are somewhat larger and radially elongated (Fig. 3).

FIG. 1.

Free-nuclear endosperm in a young *J. caffra* fruit (en—endosperm; ii—inner integument).

FIG. 2.

Periclinal division in an endosperm nucleus showing the formation of the cell plate.

FIG. 3.

Cellular endosperm in the immature fruit of *J. caffra* (en—endosperm; ii—inner integument; oi—outer integument; t—tanniferous layer).

The endosperm cell walls in an immature fruit are thin. As the fruit matures, the cellulose walls become only slightly thicker (Fig. 4) but never become as thick as the walls of the endosperm in *Phoenix dactylifera* (Lloyd, 1910). In a transverse section through the endosperm kernel, the cells are radially elongated, but in tangential section they are more or less isodiametric (Figs 4A & B). The cells of the mature endosperm are filled with droplets of oil and rhomboidal crystals.

The findings of this study regarding the absorption of the central mass of cell sap prior to maturation of the fruit, are contrary to those of Story (1959) who states that the mature fruit contains liquid endosperm or "milk", but confirms the view of Marloth (1915) who reports that the mature *J. caffra* fruit is without "milk".

Embryogeny

The data obtained in this respect are discussed below in terms of the embryonomic "classification systems" of both Johansen (1950) and Souéges (Crété, 1963).

It is felt necessary though that the systems themselves be briefly considered prior to applying them to the results of this study.

Both systems are based on the same embryonomic laws and principles and both make use of the tetrad structure and the role of the basal cell, cb, of the 2-celled proembryo in the construction of the embryo and its components as criteria for distinguishing between the various embryonomic types. One can but agree with Johansen (1950) when he regrets that these two systems (which were developed concurrently and independently of each other) were not incorporated into one.

It is not possible, and would certainly at this stage, be unwise to say which of these two systems is the better.

That of Johansen (1950) is excellent in that basically it is a relatively simple system and includes only six types of embryonomic development. These differ from each other with respect to the structure of the proembryo tetrad in the second cell generation and in the role played by the basal cell of the 2-celled proembryo in the construction of the embryo proper and its basic constituents. Each of these six types are in turn divided into an unspecified, and theoretically, unlimited number of variations.

The latter aspect is perhaps the weakness in Johansen's system. He admits that

FIG. 5.

Fertilization of the egg cell by the male gamete (fn—female nucleus; mn—male nucleus).

FIG. 6.

A—F—Longitudinal sections through proembryo at various stages of development (cf. Fig. 7). G—Longitudinal section through an embryo showing differentiation of the plumule and radicle tip. H—Transverse section through an embryo at a similar stage of development as the embryo depicted in Fig. 6G. I—Longitudinal section through a mature embryo. (c—cotyledon; pl—plumule; pc—procambium; r—radicle; rc—rootcap; sy—synergid; z—zygote).

FIG. 5

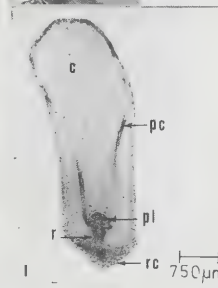
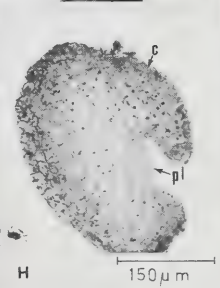
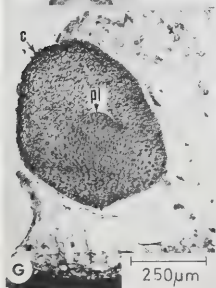
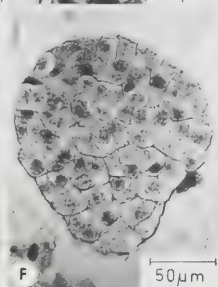
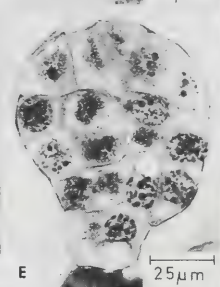
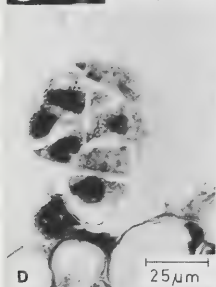
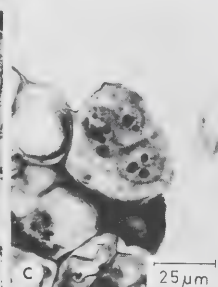
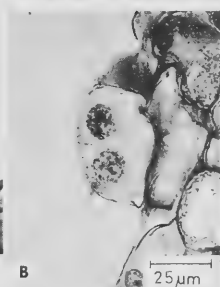


FIG. 6

not all variations are clearly definable and that some should in fact be dropped and that the species classified therein be added to some other variations. This system, it would seem, is thus not completely stable and will probably undergo various changes as more embryological data on more species become available.

Souéges' system is a very complex one and involves an unlimited number of periods, each of which is subdivided into six different groups or megarchtypes depending on the role played by the basal cell of the 2-celled proembryo in the formation of the embryo proper. Each of the megarchtypes is in turn subdivided into eight series and subseries on the basis of the proembryo tetrad formation and structure.

The disadvantage of this system is that it is too complex and clumsy. Its major advantage however, is that it is a stable system which provides for the incorporation of any future data without the basic layout or design of the system having to be changed.

Fertilization (Fig. 5) of the egg cell of *J. caffra* by one of the male gametes results in the formation of a zygote (Figs 6A & 7A) which undergoes a rest period of between 30 and 70 days (Fig. 9). During this time, division of the primary endosperm nucleus occurs. The zygote is surrounded by a thin cellulose membrane and is spherical in shape. Degeneration of the one remaining synergid becomes evident from this stage onwards.

First Cell Generation

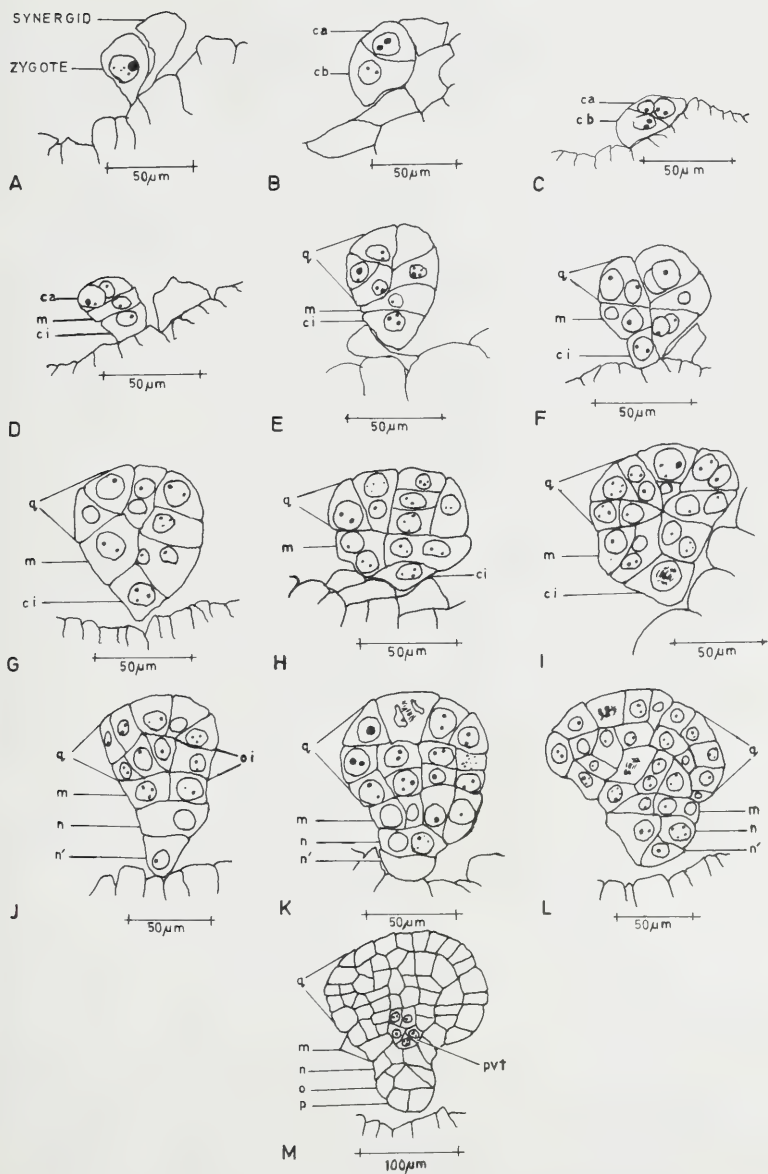
As is the case in virtually all investigated Angiosperms (Maheshwari, 1950) the first division of the zygote is transverse (Figs 6B, 7B), resulting in a proembryo comprised of two superposed cells, viz. a terminal cell and a basal cell. Being of the first period, these cells are designated ca and cb respectively. (The terminal cell refers to that one which is orientated furthest away from the micropyle while the basal cell is the cell closest to the micropyle.) This stage (Fig. 8A) represents the first cell generation.

Second Cell Generation

This generation, which is governed by the law of dispositions, is the most important with regard to the establishment of the embryonic type of *J. caffra*, because it is the generation in which the proembryo tetrad is formed. The terminal cell, ca, divides longitudinally and consequently a three-celled proembryo is formed. This proembryo consists of two juxtaposed cells in the upper tier and the single basal cell, cb in the lower tier (Figs 6C, 7C). Shortly thereafter, cb divides transversely to produce two superposed daughter cells m and ci. At this stage the proembryo is comprised of four cells arranged in three tiers, viz. ca, comprising two cells and tiers m and ci, each consisting of a single cell (Figs 7D, 8B). This

FIG. 7.

Diagrammatic representation of embryogeny of *J. caffra*.



stage constitutes the proembryo tetrad of the second cell generation. The structure of this tetrad makes it possible at this stage to classify the embryonic type as being either of the Onagrad or the Asterad Types (Johansen, 1950). In terms of Souéges' periodic megarch system, the tetrad would belong to the first period of the A2 (filamentous) series.

Third Cell Generation

Although this generation is usually characterized by eight cells, the law of numbers often intervenes to bring about variations (Maheshwari, 1963).

The two cells in the upper tier (ca) of the tetrad divide by means of longitudinal walls to produce a single tier q, of four cells.

The middle cell m, also undergoes a longitudinal division to form a two-celled tier while tier ci remains undivided (Figs 7E, 7F).

In some cases the divisions resulting in the formation of q precede those in tier m, while in other cases, m divided before the cells in the upper tier (cf. Figs 7E, 7F).

Thus the third cell generation of *J. caffra* consists of seven cells arranged in three tiers, viz. q (four cells), m (two cells) and ci (one cell) (Fig. 8C).

Fourth Cell Generation

The quadrant cells of tier q in the third cell generation each divide by a transverse wall (Figs 7G, 7H) to produce an octant consisting of two tiers (oi and os) of four cells each. Concurrently the two cells constituting tier m in the third cell generation (Fig. 8C) both divide longitudinally (Fig. 7G) to produce a 4-celled tier (Fig. 7H). Division of the single cell ci is somewhat retarded, but it does eventually divide transversely (Fig. 7I) to produce two superposed tiers, viz. n and n' (Fig. 7J).

The proembryo constituting the fourth cell generation thus originates by the bipartitioning of each of the seven cells in the third cell generation and consequently it is comprised of 14 cells arranged in five tiers (Fig. 8D).

From the fourth cell generation onwards, the number of cells makes it extremely difficult to follow the precise pattern of cell divisions. It is possible though to follow the general development of each of the tiers, i.e. q, m, n and nw.

The cells of tier oi (Fig. 7J) divide transversely so that q consists of three tiers (Figs 6E, 7K). Thereafter, cell division in both oi and os occurs in both peri- and anticlinal directions and it becomes impossible to demarcate each tier of cells in q. At this stage a series of anticlinal divisions results in the formation of the dermatogen (Fig. 7L).

Cell divisions in tiers m, n and n' do not occur at the same rate as in q and no further divisions occur in these three tiers until the upper half of the proembryo is well developed (Fig. 7L). Subsequently n' divides transversely to produce two cells. The upper of these daughter cells constitutes tier o while the lower forms tier p. (Fig. 7M). Following this, the cells in p, o and n divide longitudinally while

those in m divide both longitudinally and transversely. It is at this stage that the first signs of differentiation of the stem's growth point, pvt, become evident in tier m (Figs 6B & 7M).

It is possible to predict the destinations of the various tiers which constitute the proembryo at this point. The growth point, the initials of the central cylinder of the root and the hypocotyl all originate from tier m while p forms the suspensor. Tier o will produce the root cap and the cells in tier n give rise to the initials of the root cortex while tier q produces the cotyledon.

The best way to summarize the embryonomy of *J. caffra* is by means of a recapitulatory table for the first four cell generations (using the abbreviations as prepared by Johansen (1950)).

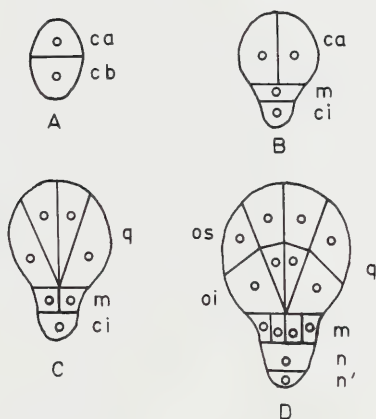


FIG. 8.

Schematic representations of the first four cell generations during the embryogeny of *J. caffra* flattened into a single plane. A—First cell generation; B—Second cell generation; C—Third cell generation; D—Fourth cell generation.

1. First Cell Generation (Fig. 8A)

Proembryo of two cells disposed in two tiers:

ca = pco

cb = phy + pvt + icc + iec + co + s

Second Cell Generation (Fig. 8B)

ca = pco

m = phy + pvt + icc

ci = iec + co + s

Third Cell Generation (Fig. 8C)

Proembryo of seven cells disposed in three tiers:

$$q = pco$$

$$m = phy + pvt + icc$$

$$ci = iec + co + s$$

Fourth Cell Generation (Fig. 8D)

Proembryo of 14 cells disposed in four tiers:

$$q = pco$$

$$m = phy + pvt + icc$$

$$n = iec$$

$$n' = co + s$$

It is clear from the above data that the basal cell *cb*, of the two-celled proembryo plays a substantial role in construction of the embryo components and consequently the embryonomy of *J. caffra* is of the Asterad Type and not the Onagrad Type (Johansen, 1950). The closest applicable variation of this type is the *Muscari* Variation (Johansen, 1950).

However, in the typical *Muscari* Variation, division of *ci* into *n* and *n'* occurs during the third cell generation. So, too, the division of *n'* into *o* and *p* take place during the course of the fourth cell generation. The third cell generation of *Muscari* therefore consists of eight cells in four tiers and the fourth cell generation of 16 cells in five tiers. Consequently the recapitulatory table for these two generations of *Muscari* are as follows:

$$\begin{aligned} 3. \quad & q = pco \\ & m = phy + pvt + icc \\ & n = iec \\ & n' = co + s \end{aligned}$$

$$\begin{aligned} 4. \quad & q = pco \\ & m = phy + pvt + icc \\ & n = iec \\ & o = co \\ & p = s \end{aligned}$$

(Johansen, 1950)

As already mentioned above, the formation of tiers *n* and *n'* from *ci* is retarded in *J. caffra* and delayed until the fourth cell generation while the division of *n'* occurs somewhat later than the fourth cell generation. The result is that the recapitulatory tables of these two genera, i.e. *Muscari* and *Jubaeopsis* appear quite different.

The fact that the embryogeny of *J. caffra* and *Muscari* is basically the same, but

that they differ with respect to cell numbers in the third and fourth cell generations as shown in their recapitulatory tables, raises two questions.

Firstly, to what extent should the embryogeny of two species differ before they can be classified into two different variations? Secondly, can the creation of a new variation of Asterad Type for *J. caffra* be justified?

The first question reflects the weakness of Johansen's system because no fixed criteria exist. The creation of a new variation would depend entirely on the personal opinion of the individual researcher and consequently no standard application of the system is possible.

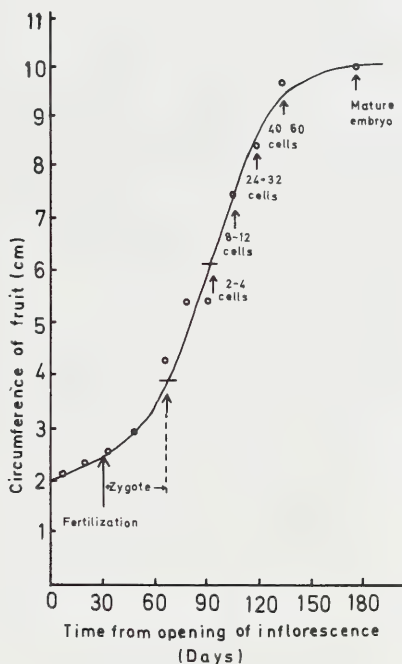


FIG. 9.

Fruit growth in relation to the development of the embryo of *J. caffra*.

It is in this respect that Souéges' system of an infinite number of periods and six basic megarchtypes is perhaps to be preferred. The megarchtypes are defined on the basis of the destination of the basal cell of the two-celled proembryo. Both *Jubaeopsis* and *Muscari* are of the first period, both belong to Megarchtype 1 where $cb = pvt + phy + icc + iec + co + s$ and both have a series A2 tetrad, (i.e. T-shaped) in the second cell generation. Consequently their embryogeny is

essentially the same and it is felt that in the event of their embryonomy being classified according to Johansen's system, they both be placed in the same variation, viz. the *Muscari* Variation of the Asterad Type.

Initially the development of the proembryo is extremely slow. As mentioned earlier, and as reflected in Fig. 9, the zygote undergoes a rest period of between 30 and 70 days. During this time though, fruit and endosperm development continues unabated.

By the time that the proembryo tetrad is formed, i.e. 90 days after the opening of the inflorescence, the fruit has already reached 60 per cent of its mature size (Fig. 9). During the next 45 days, development in the proembryo is somewhat faster, but still remains slow in relation to fruit development and by the time that the fruit has reached approximately 95 per cent of its final size, the proembryo exists as an undifferentiated, more or less globular, 64-celled structure (Fig.9).

From this point on however, i.e. during the last 45 days of development, growth of the fruit virtually ceases, while growth and differentiation of the embryo increase tremendously. During this period, the growth points of both the stem and radicle become fully differentiated and the cotyledon develops.

Maturation of both the fruit and embryo is preceded by the absorption of the central mass of cell sap or "milk" which is initially present in the endospermal cavity.

CONCLUSIONS

While the majority of palms have nuclear endosperm, there seems to be some difference in the manner by which the endosperm becomes cellular. In *J. caffra* the free-nuclear condition is apparently terminated by wall formation, resulting from cell-plates. No ruminations occur.

The results of this study indicate that Story's (1959) report concerning the presence of endosperm "milk" in the mature fruit, is incorrect.

As far as the embryogeny is concerned it appears from the data accumulated in this study that it is of the Asterad Type and specifically of the *Muscari* Variation if classified according to Johansen (1950) or of the first period, Megarchtype 1 with a Series A2 tetrad in the second cell generation in terms of the system of Souéges (Crété, 1963). Unfortunately very little information with respect to the embryogeny of other palms is available and no comparisons are possible. It appears though that the embryogeny of the Palmae is very divergent and in view of the fact that such a small number of palm species have been studied in this respect, it would seem that a study of the embryogeny of genera from the various sub-families would be both enlightening and well justified.

ACKNOWLEDGEMENTS

The writer is indebted to the University of Port Elizabeth and the C.S.I.R. for their financial support of this project.

REFERENCES

- BARRY, D. JR., 1957. The African relative of the Chilean Wine Palm. *Principes* **2**: 180–2.
- BECCARI, O., 1913. Una nuova "Cocoina" africana: *Jubaeopsis caffra*. *Webbia* **4**: 169–176.
- BROOKS, R. M., BRADLEY, Muriel V. and ANDERSON, Thelda I., 1950. *Plant microtechnique manual*. Davis: University of California.
- CRÉTÉ, P., 1963. Embryo. In: P. Maheshwari (ed.), *Recent advances in the embryology of Angiosperms*. Ranchi: Catholic Press.
- CUTTER, V. M. JR., WILSON, Katherine and FREEMAN, B., 1955. Nuclear behaviour and cell formation in the developing endosperm of *Cocos nucifera*. *Am. J. Bot.* **42**: 109–115.
- DATTA, Mridula, 1955. The occurrence and division of free nuclei in the endospermal milk in some Palmae. *Trans. Bose Res. Inst.* **19**: 117–125.
- DAVIS, Gwenda L., 1966. *Systematic embryology of the Angiosperms*. New York: John Wiley & Sons, Inc.
- DUTT, Mridula, 1953. Dividing nuclei in coconut milk. *Nature* **171**: 799.
- GUIGNARD, J., 1961. Embryologie Vegetale—Embryogénie des Palmiers. Développement de l'embryon chez le *Chamaerops humilis* L. *C.r. hebd. Séanc. Acad. Sci.* **253**: 1834–1836.
- HOLTZHAUSEN, L. C., 1972. 'n Morfo-genetiese en fenologiese studie van die blom en vrug van *Citrus sinensis* (L.) Osbeck., cultivar Valencia. Pretoria: University of Pretoria. D.Sc. (Agric.) thesis.
- JOHANSEN, D. A., 1950. *Plant Embryology*. Waltham, Mass.: Chronica Botanica Company.
- LONG, F. R., 1950. Mkomba or Mkabati Palm. *Pk Adm.* **2** (1).
- LLOYD, F. E., 1910. Development and nutrition of the embryo, seed and carpel in the Date, *Phoenix dactylifera* L. *Rep. Mo. bot. Gdn.* **21**: 103–164.
- MAHESHWARI, P., 1950. *An introduction to the embryology of Angiosperms*. New York: McGraw-Hill Book Company.
- MAHESHWARI, P., 1963. *Recent advances in the embryology of Angiosperms*. Ranchi: Catholic Press.
- MARLOTH, R., 1915. *Flora of South Africa* **4**: 48.
- PALMER, Eve and PITMAN, Norah, 1972. *Trees of Southern Africa*. Cape Town: Balkema.
- ROBERTSON, B. L., 1976a. Embryology of *Jubaeopsis caffra* Becc. 1. Microsporangium, microsporogenesis and microgametogenesis. *Jl S. Afr. Bot.* **42**: 97–108.
- ROBERTSON, B. L., 1976b. Embryology of *Jubaeopsis caffra* Becc. 2. Megasporangium, megasporogenesis and megagametogenesis. *Jl S. Afr. Bot.* **42**: 173–184.
- ROBERTSON, B. L. and VISAGIE, G. P., 1975. *Jubaeopsis caffra*—An Eastern Cape Rarity. *The Eastern Cape Naturalist* **55**: 15–19.
- SASS, J. E., 1958. *Botanical microtechnique*. Iowa: Iowa State University Press.
- STORY, R., 1959. The Pondoland palm. *Principes* **3**: 103–106.
- VENKATA RAO, C., 1955. Embryological studies in Palmae III. *Proc. 42nd Indian Sci. Congr.* **3**: 232.
- VENKATA RAO, C., 1958. Contributions to the embryology of Palmae. *J. Indian bot. Soc.* **38**: 46–75.
- WAGER, V., 1958. *Project report (Ntafufu-Mboyti) by the Natal Fieldwork Section of the Wildlife Protection and Conservation Society*. Durban.
- WICHT, H., 1969. *The indigenous palms of Southern Africa*. Cape Town: Howard Timmins.